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Formation of maternal trophic structures for embryos of *Paruroctonus mesaensis* (Scorpionida: Vaejovidae)

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Formation of maternal trophic structures for embryos of *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). - The female reproductive system is located within the mesosoma and consists of interconnected longitudinal and transverse tubules (ovariuterine). Anteriorly, these are joined to paired oviducts and the genital operculum on the ventral surface of the first mesosomal segment. Earlier studies showed the ova differentiate from an inner germinal epithelium of the ovariuterine tubules. The present results suggest each ovum influences the differentiation of nearby cells so they give rise to structures that nourish the ovum and, eventually, the embryo. Each ovum, with follicle cells, forms a protuberance (follicle) on the surface of the ovariuterine tubules. After fertilization, the ova pass back into the the ovariuterine tubule (ovulation) where the embryos enlarge, attached to a cell mass that is part of a trophic network. The cell mass is probably a follicular placenta derived from follicle cells inside the protuberance. Secondary trophic cells associated with the ovum, but outside the protuberance, migrate along the surface of the tubules and eventually form a trophic tubular network, parallel and attached to the ovariuterine tubules. Many ova, initially separated by tenths of a millimeter, fail to develop so that embryos are later separated by one or more millimeters. Scorpions have a complex circulatory system, but matrotrophic development is sustained not by specialized vascularization but by structures derived from ovariuterine cells associated with the ova.

Key-words: Scorpions - *Paruroctonus mesaensis* - Follicle cells - Placenta - Development - Matrotrophic development - Ovariuterine tubules - Viviparity - Follicular placenta.

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INTRODUCTION

The reproductive system of female scorpions is in the mesosoma (body somites X-XVI) where a network of longitudinal and tranverse tubules is intermingled with lobules of the digestive gland (HJELLE 1990; FARLEY 1996a). Anteriorly, the reproductive tubules are connected to a pair of oviducts that expand into seminal receptacles and then join to form a single genital chamber with an opening (gonopore) on the ventral surface of the first mesosomal segment. Externally, the gonopore is covered by a genital operculum.

Ova develop from cells in the inner epithelium of the reproductive tubules (LAURIE 1890; PAWLOWSKY 1924, 1925; PFLUGFELDER 1930; AWATI & TEMBE 1956; MATHEW 1959, 1962; MAKIOKA 1992), but the tubules are also the site of embryogenesis and provide a conduit for passage of mature embryos during parturition. Authors initially referred to the tubules as ovarian, but later designated them as ovariuterine in recognition of their multiple function (PAWLOWSKY 1924, 1925; PFLUGFELDER 1930; FRANCKE 1982; HJELLE 1990).

MATHEW (1962) described how the germinal epithelium produces ova and follicle cells, then later disappears as the embryos mature and the tubules are used for passage of the embryos to the gonopore. Histological sections of the tubular wall showed muscle cells that probably cause egress of the embryos. The germinal epithelium is later restored; ova and follicle cells are differentiated among other cells of the epithelium; and fertilization, embryogenesis and parturition are repeated for another generation.

LAURIE 1896*a*, *b*) first recognized that scorpions have two general patterns of development. In the Scorpionidae and Diplocentridae, each embryo develops within a specialized diverticulum of the ovariuterine tubules. This was termed katoikogenic (*Greek*, at home) development by LAURIE (1896*b*) and subsequent workers (PAWLOWSKY 1924, 1925; PFLUGFELDER 1930; WERNER 1934; VACHON 1950; ROSIN & SHULOV 1962; POLIS & SISSOM 1990; WARBURG & ROSENBERG 1990; FARLEY 1996*a*, *b*). In the Buthidae, Bothriuridae, Chactidae, Iuridae and Vaejovidae, embryos commonly develop within successive enlarged regions of the ovariuterine tubules (apoikogenic, away from home), with little specialization and modification of the tubules (LAURIE 1890, 1896*a*, *b*; BRAUER 1895; WERNER 1934; PAVLOVSKY 1924, 1925; POLIS & SISSOM 1990; WARBURG & ROSENBERG 1990; FARLEY 1996*a*, *b*).

Development in the vaejovid, *Paruroctonus mesaensis*, is apoikogenic, but more complex than that described above (FARLEY 1996*a*, *b*). In this species, each embryo is attached to a trophic cell mass within a specialized region (uterus) of the reproductive tubules. The cell mass is a placenta, according to modern usage (MOSSMAN 1937; WOURMS & LOMBARDI 1992), and is part of a network of trophic tubules that develops parallel and attached to the ovariuterine tubules (FARLEY 1996*a*, *b*). As shown in the present study, the trophic structures arise from ovariuterine cells that are initially in close proximity to the ova.

Development in *P. mesaensis* is a striking example of a general pattern in scorpions. Ovariuterine cells associated with the ovum have much adaptive potential

and, among the various taxa, form a diversity of structures for embryo nourishment (Pflugfelder 1930; Matthew 1965; Vachon 1950; Makioka 1992; Farley 1996*b*). This elaboration of ovum support-cells in scorpions contrasts with many viviparous fish and other vertebrates where embryos are sustained by placentae that are densely filled with maternal blood vessels (Wourms 1981; Wourms *et al.* 1988; Blackburn 1992; Stewart 1992; Wourms & Lombardi 1992).

MATERIAL AND METHODS

The composition of physiological saline and the procedures for collection and maintenance of specimens of *Paruroctonus mesaensis* (Stahnke 1957) were described in an earlier publication (Farley 1987). Tissues were flushed with saline to remove debris as animals were dissected with microscissors and forceps. Ovariuterine tubules were removed from immature (second year) and adult, gravid females in their third or later year (Polis & Farley 1979). In some females with advanced embryos, the tubules were teased open so the embryos and trophic tissues could be examined with the electron microscope.

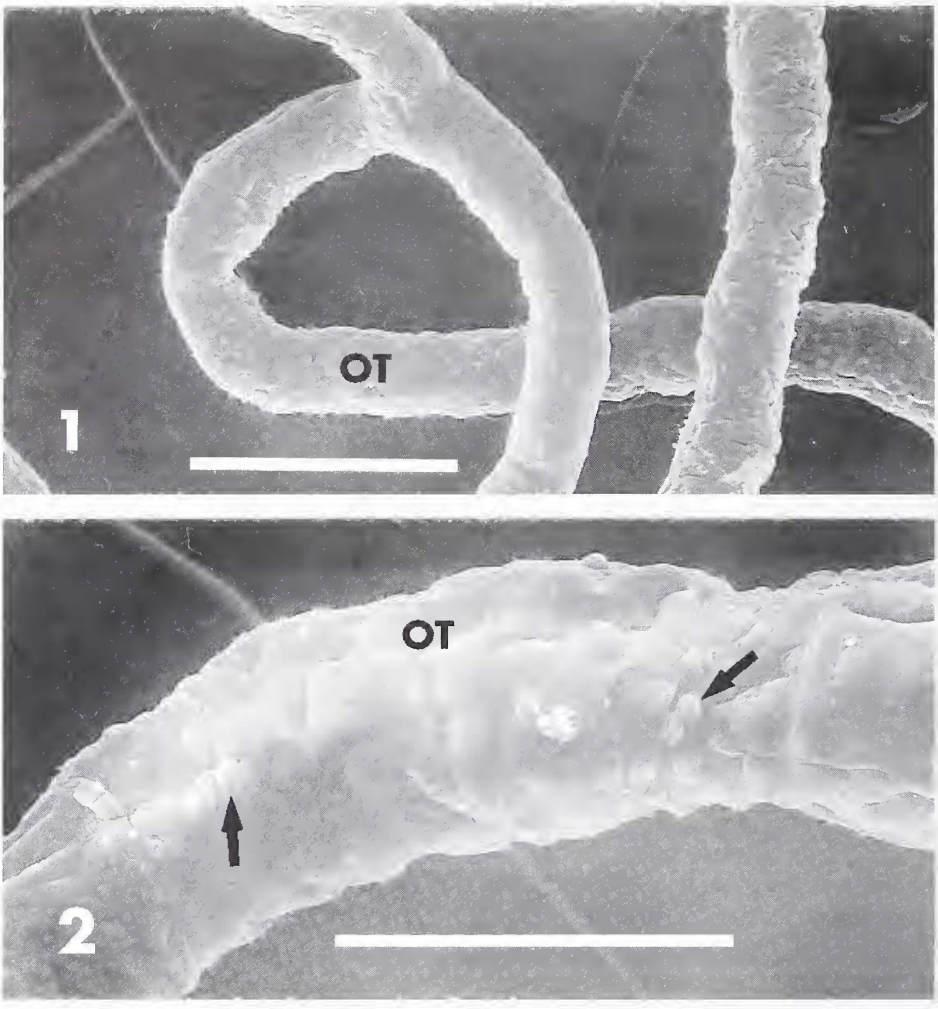
Tissues were fixed (6–10 hrs, 23–25°C) with 4% glutaraldehyde in 0.1 M cacodylate buffer with one drop of $CaCl_2$ for each 10 ml of solution. The tissues were washed in cacodylate buffer-NaCl solution and postfixed (2 hr, 23–25°C) in 1% OsO_4 in 0.2 M cacodylate buffer with NaCl. The concentration of these solutions was adjusted to approximate the osmolality of scorpion blood (630 mOsm; Yokota 1984). Tissues were dehydrated in acetone, critically-point dried (Balzers, CDD 020) and sputter-coated (Emscope SC500) with 20 nm thickness of gold/palladium. Tissues were examined at 12–15 KV with a Philips 550 scanning electron microscope.

RESULTS

As in other female scorpions, the ovariuterine tubules of *P. mesaensis* are intermingled with the massive digestive gland that occupies most of the space of the mesosoma (Farley 1996*a*). At some places along their length, the tubular surface is attached by connective tissue to the external sheath of the digestive gland. The delicate tubules are easily severed during dissection, but examination of tissues from immature, second-year females shows that initially there are single tubules without follicle cells on the surface or ovum protuberances (Fig. 1).

In the ovariuterine tubules of Figure 2, the external surface shows early indications that ova and trophic cells have differentiated inside and are about to move to the outside and form a protuberance (follicle). At regular intervals (0.2–0.3 mm), there is a narrowing of the tubule, and large cells appear on the surface as though they are migrating from the inside. These cells (herein designated as secondary trophic cells) are clearly associated with the ovum but are outside the protuberance that later appears on the surface (Fig. 3).

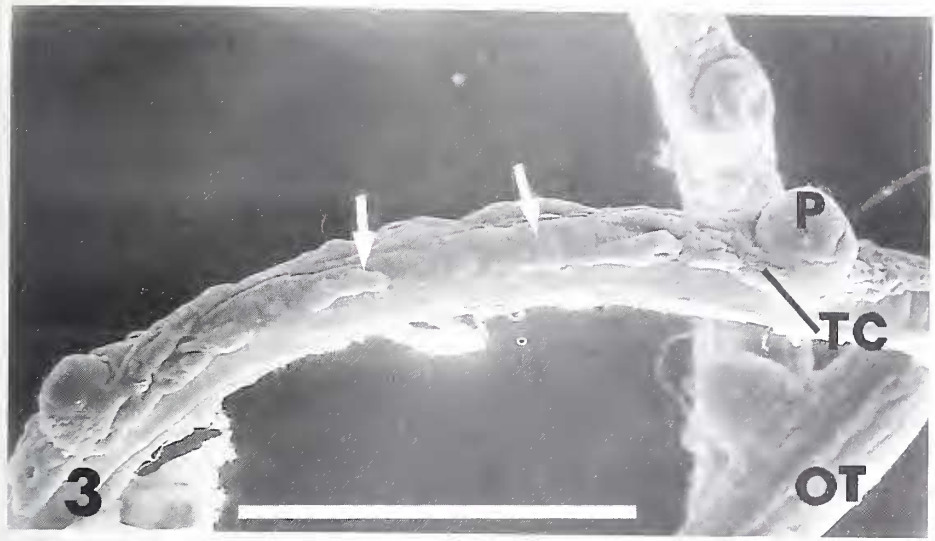
A column of follicle cells accompanies the ovum as it forms the protuberance (Laurie 1890; Awati & Tembe 1956; Warburg *et al.* 1995), and a thin follicular

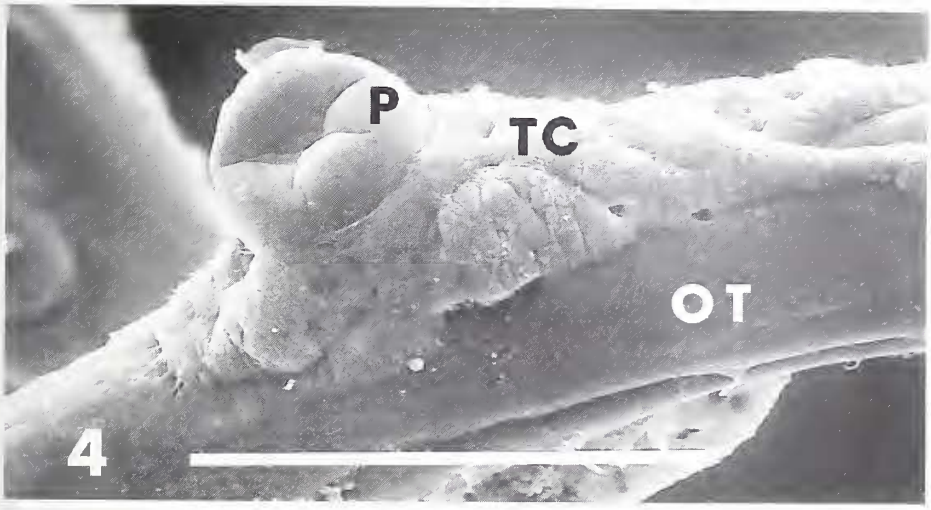


FIGS 1–2

Fig. 1: In immature, second-year females, the reproductive system has longitudinal and transverse ovariuterine tubules (OT) that are relatively smooth and undifferentiated on their surface. Scale, 0.3 mm. Fig. 2: Narrowing of the ovariuterine tubules (OT) at regular intervals indicates sites where ovum protuberances (follicles) eventually form. Large cells evident near the surface (arrows) are secondary trophic cells. Scale, 0.1 mm.

layer surrounds the ovum. These intra-protuberal follicle cells are herein labeled primary trophic cells to distinguish them from cells associated with the ovum but outside the protuberance (Figs 2–4). At a later stage, probably after fertilization, the ovum passes back into the ovariuterine tubule (ovulation; Schroeder & Talbot 1985) where the embryo develops. Ovulation may have occurred from indented protuberances (Figs 3, 4), leaving follicle cells inside the sheath.

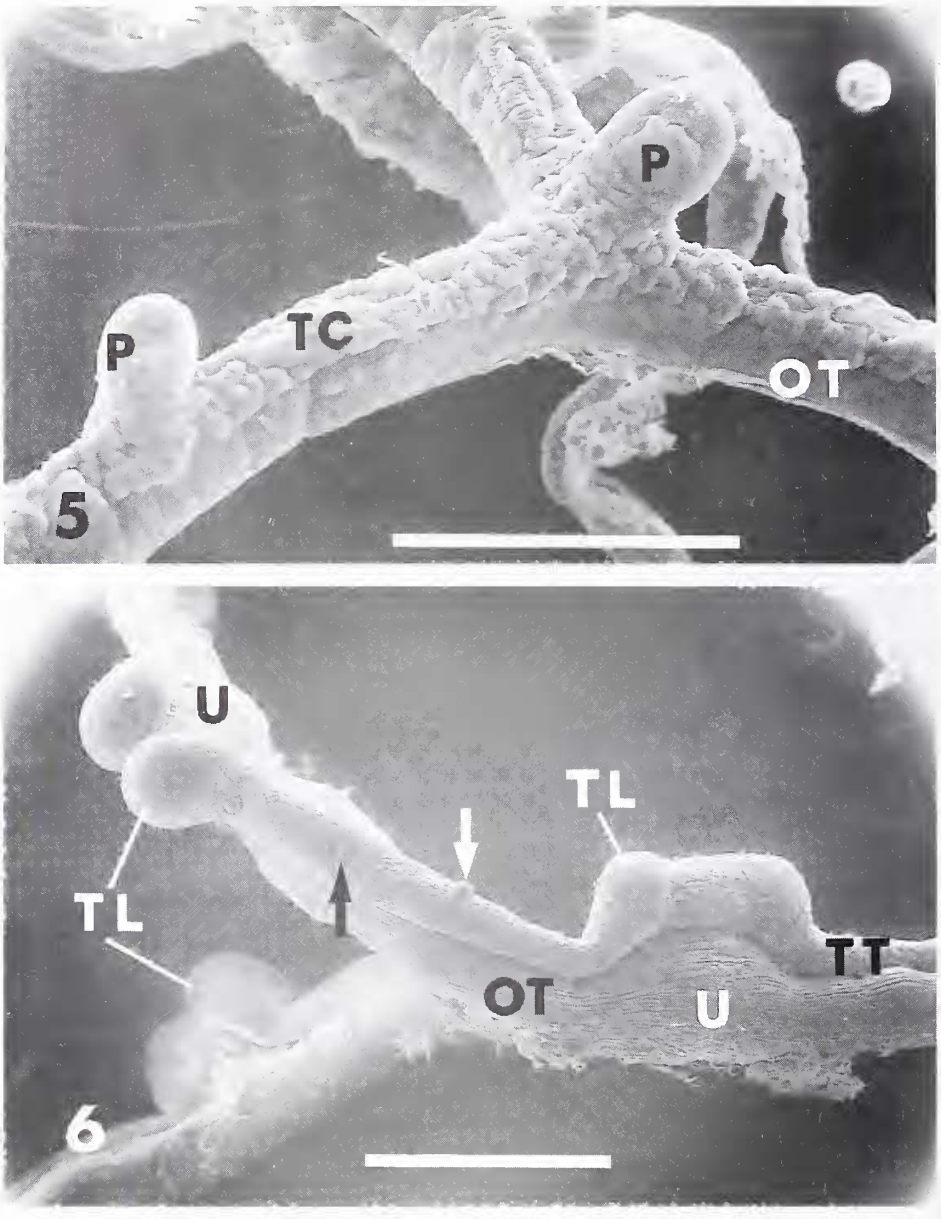




FIGS 3–4

Fig. 3: Ovum protuberances (P) on the surface of ovariuterine tubules (OT) have secondary trophic cells (TC) clustered at their base. From this initial location, the cells migrate (arrows) along the surface of the tubule. Scale, 0.2 mm. Fig. 4: Protuberance (P) with indentation, possibly resulting from ovulation, *i.e.* passage of the fertilized ovum back into the ovariuterine tubule (OT). Secondary trophic cells (TC) are clustered at base of protuberance. Scale, 0.1 mm.

As the ovum protuberances appear initially on the surface, secondary trophic cells can be seen at their bases (Figs 3, 4). These cells migrate along the outside of the ovariuterine tubule (Fig. 3), forming a continuous layer (Fig. 5).



FIGS 5–6

Fig. 5: Secondary trophic cells (TC) have formed a continuous layer between protuberances (P) and attached to the ovariuterine tubule (OT). Scale, 1 mm. Fig. 6: Early stage in formation of trophic lobe (TL) at site of embryogenesis. The enlarging embryos form swellings (U, uterus) in the ovariuterine tubule (OT). The trophic tubule (TT), derived from secondary trophic cells (Figs 3–5), thickens and forms a pair of lobes above the uterus. The two lobes increase in size, merge together (two examples at left) and become a single lobe (Fig. 8). Arrows indicate remnants of ovum protuberances nearly covered by trophic cells. Swellings beneath remnants suggest some embryogenesis, but continuation is unlikely without trophic lobes. Scale, 0.1 mm.

The secondary trophic cells eventually surround and cover most of the protuberances (Figs 5, 6), and many of these sites do not show further signs (e.g. tubular enlargement) of embryogenesis. There also appears to be competition for space among those embryos that do begin enlarging (Fig. 7). Many embryos are initially present, but development continues only in those separated a millimeter or more.

Each embryo develops within a specialized region (uterus) of the tubules (Figs 6–9). The uterus consists of an enlarging region with paired trophic lobes derived from the layer of secondary cells. Figure 6 shows an early stage in the formation of trophic lobes: the follicular layer is thickening just above the uterus with its enclosed embryo.

In most apoikogenic scorpions, the embryos enlarge within the ovariuterine tubules with little modification and specialization of the latter (Farley 1996*a*, *b*). The tubule simply enlarges at the site of each growing embryo. In *P. mesaensis*, one side (lateral mesosoma) of the embryo eventually abuts a mass of trophic cells (Farley 1996*a*, *b*) that are attached to the uterine trophic lobes (Fig. 8). In Figure 9, the embryo chamber was opened to show the enlarging trophic cell mass. At this stage (bastula or gastrula), the embryo is not yet attached to the cell mass and is easily washed from the uterus during preparation for microscopy.

The embryo is eventually enclosed within a thin amnion, and a thicker serosa surrounds the embryo, amnion and trophic cell mass (Farley 1996*a*, *b*). The scanning electron microscope was used to examine the trophic mass and lobes (Figs 8, 9) after they were opened by dissection. They appeared to consist entirely of cells with no indication of vascularization. After cutting the serosa, the embryo is easily separated from the trophic mass, since there are no interconnecting blood vessels or fibrous tissue (Fig. 10).

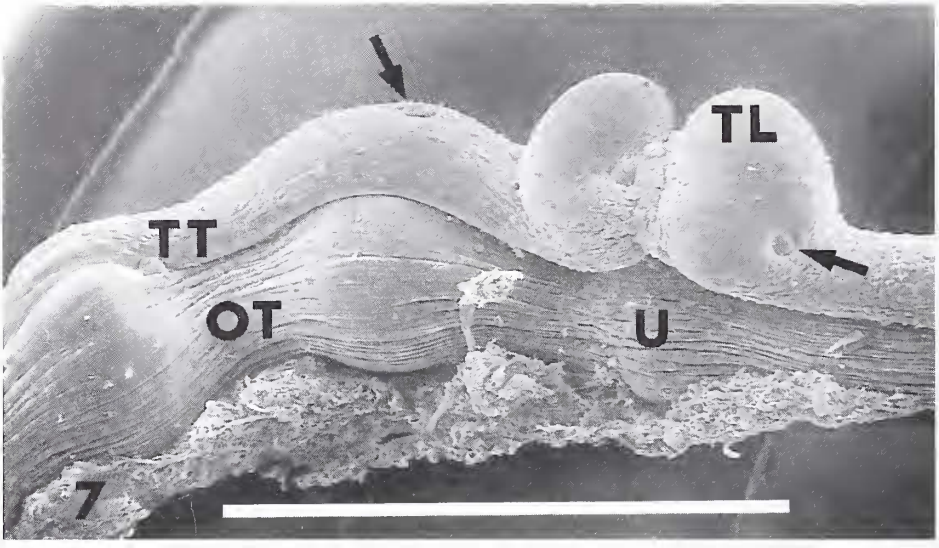
DISCUSSION

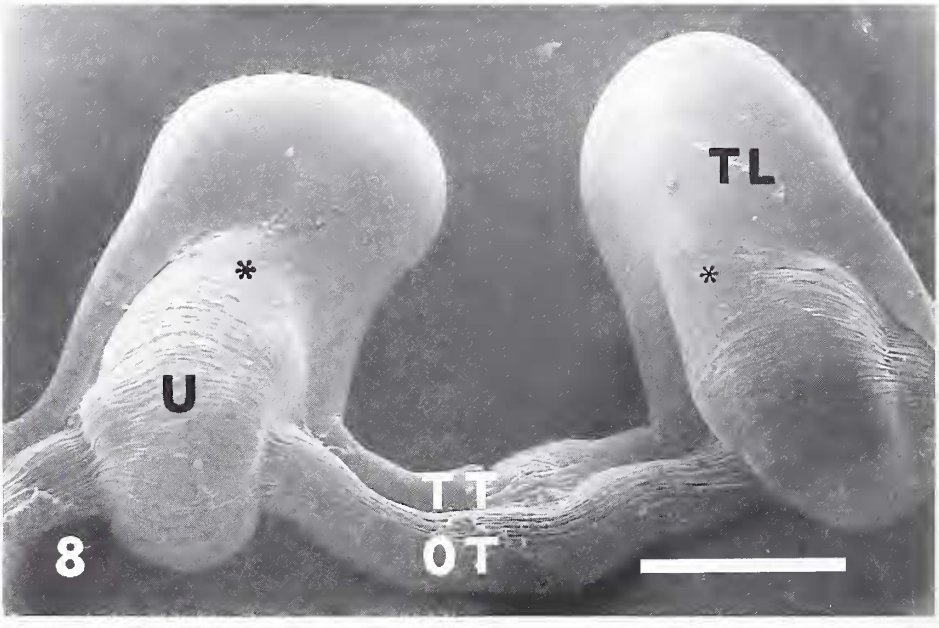
Formation of the Trophic System

The results in this study suggests that within the ovariuterine epithelium, each ovum influences the differentiation of nearby cells so they give rise to structures that support the ovum and, eventually, the embryo. The differentiation depends on initial distance from the ovum, as though a chemical gradient is involved. Two separate lineages give rise to trophic structures that eventually merge into a single network.

Primary trophic (follicle) cells form the column of each protuberance and a thin layer surrounding the ovum (Laurie 1890; Awati & Tembe 1956; Warburg *et al.* 1995). After fertilization, ovulation and return of the ovum into the tubule (Fig. 4), the follicle cells are in a position to give rise to the trophic cell mass that later abuts the developing embryo (Figs 8–10; Farley 1996*a*, *b*).

Secondary trophic cells appear on the surface of the tubules before or at the same time as the initial bulge of the protuberance (Fig. 2). These cells later appear at the base of the protuberance (Figs 3, 4), outside its sheath, as though they migrated to the surface with the protuberance. The secondary trophic cells sequentially form: a





FIGS 7–8: 7. Developing embryos compete for space. For embryo at right, continuation is likely in uterus (U) with trophic lobes (TL). Two swollen regions at left indicate embryos in ovariuterine tubule (OT), but the absence of trophic lobes suggests cessation and reabsorption (*i.e.* the embryos are not sufficiently spaced to allow maturation). Arrows indicate tops of ovum protuberances nearly covered by cells of the trophic tubule (TT). Scale, 1 mm. Fig. 8: Swellings in the ovariuterine tubule (OT) indicate developing embryos within uteri (U), each with a trophic lobe (TL) formed from the trophic tubule (TT). Inside each uterus, the embryo abuts a trophic cell mass (*), evident in the opened uterus of Figure 9. Scale, 0.5 mm.

continuous layer (Figs 3, 5), trophic tubules (Figs 6–8), and, at each uterus, a pair of trophic lobes (Figs 6, 7) that merge to become a single lobe (Figs 8, 9).

Follicular Placenta

As the embryo develops, one side of the mesosoma is pressed against the trophic cell mass (Fig. 9; FARLEY 1996*a*, *b*). The morphology suggests the latter functions as a placenta (MOSSMAN 1937; WOURMS & LOMBARDI 1992) and is derived from follicle cells. Follicular placentae are present in some fish (GROVE & WOURMS 1991; WOURMS & LOMBARDI 1992) and dermapteran insects (HAGAN 1951).

In *P. mesaensis*, the placenta and attached embryo are enclosed within a serosal membrane (Fig. 10) that holds the embryo securely against the trophic cells. The embryo stomodeum develops relatively late in this and other apoikogenic species (POLIS & SISSOM 1990; FARLEY 1996*a*, *b*), so nutrients are probably absorbed through the integument. The serosa confines placental secretions to the vicinity of the embryo and may transfer additional nutrients from the uterine wall (Fig. 9).

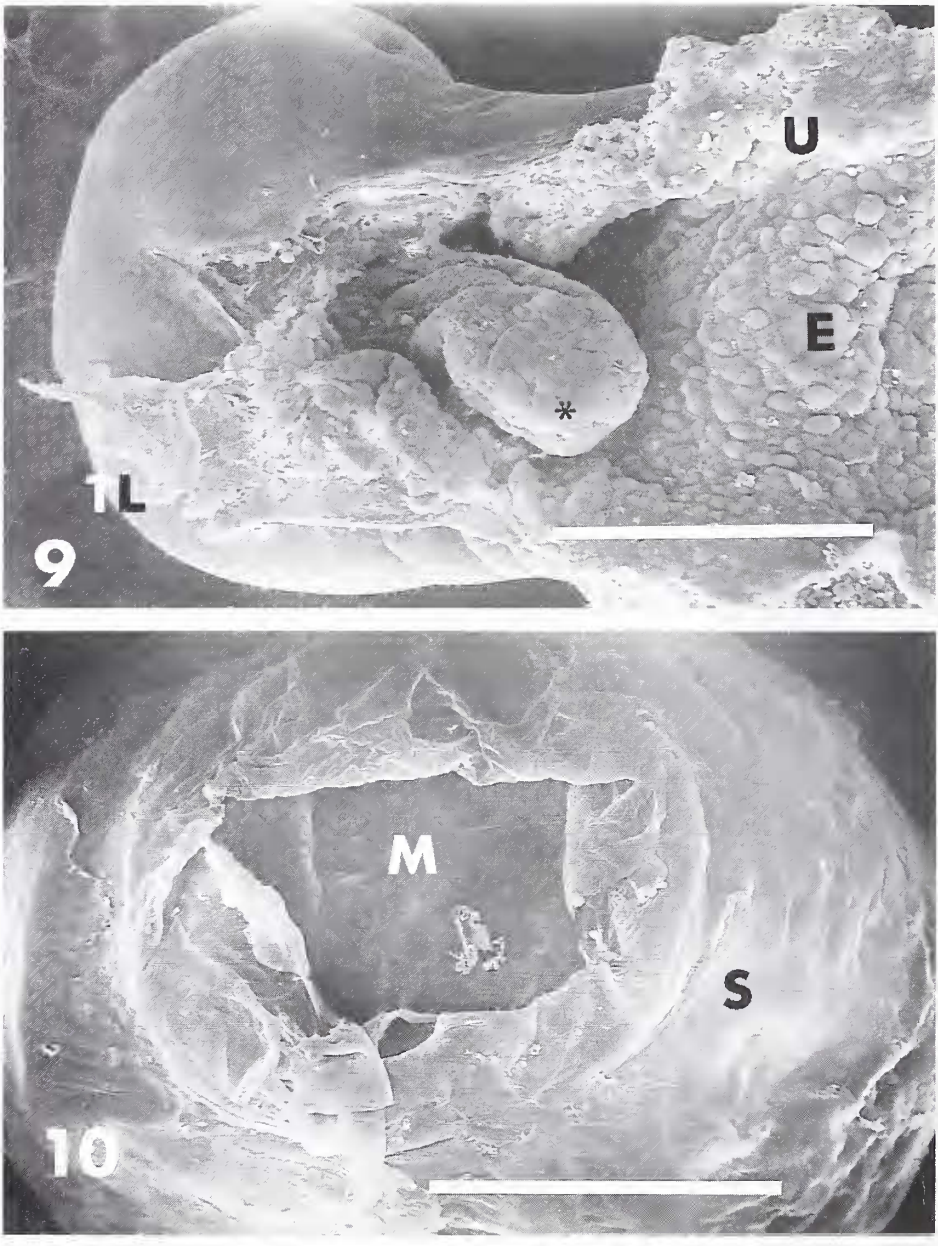
In adult, and probably embryonic scorpions, the lateral mesosoma has large segmental veins (pneumocardial) that carry blood from the booklungs (ventral mesosoma) to the pericardial sinus and heart in the dorsal mesosoma (FARLEY & CHAN 1985; FARLEY 1990*a*, *b*). Thus, even without additional vascularization, the attachment of the embryo at its lateral mesosoma should facilitate distribution of nutrients absorbed from the placenta.

Comparison of Trophic Structures

A diversity of structures for embryo nourishment is described for females of different scorpion taxa (POLIS & SISSOM 1990; WARBURG & ROSENBERG 1990; FARLEY 1996*b*). A common pattern is that these structures are formed from ovum support-cells rather than vascular specializations.

In the Scorpionidae and Diplocentridae (SISSOM 1990; POLIS & SISSOM 1990), the ova are retained within protuberances and do not return to the lumen of the ovariuterine tubule. The protuberances increase in size, becoming diverticulae that enclose the enlarging embryo (katoikogenic development). At the tip of each diverticulum, a tubular appendix has morphology that suggests it absorbs and channels maternal nutrients to the mouth of the embryo (PFLUGFELDER 1930; MATHEW 1965; VACHON 1950; MAKIOKA 1992). Based on their histological studies, these authors report that the appendix is formed from follicle or other cells near the ovum at the tip of the diverticulum.

Scorpions have a complex circulatory system (LANE *et al.* 1981; FARLEY & CHAN 1985; FARLEY 1990*a*, *b*), but it is unclear why this system has so little specialization for embryo nourishment, based on studies so far. Ovariuterine cells associated with the ova, rather than vascular adaptations, provide the basis for matrotrophic diversity. This is in contrast to viviparous fish and other vertebrates where vascularized placentae are common (WOURMS 1981; WOURMS *et al.* 1988; BLACKBURN 1992; KING 1992; STEWART 1992; WOURMS & LOMBARDI 1992).



FIGS 9–10: 9. Opened uterus (U) showing early stage in formation of trophic cell mass (*) that becomes a placenta abutting lateral mesosoma of embryo. The embryo and placenta are not yet enclosed in a serosa, so the embryo was removed during tissue preparation. The trophic cell mass is attached to trophic lobe (TL). The uterine epithelium (E) is probably important for nutrient transfer, especially before the placenta forms. Scale, 0.5 mm. Fig. 10: Lateral mesosoma (M) of embryo viewed through opening in serosa (S). The serosal opening is the site where the embryo abutted the placenta (not shown). After cutting the serosa, the embryo is easily separated from the placenta since there are no interconnecting blood vessels or fibrous tissue. Scale, 0.5 mm.

Without vascularization, the length and distribution of scorpion matrotrophic tissues are probably important in providing surface area for absorption. In scorpions with katoikogenic development, the appendix is a separate tubule, unsupported distally and relatively short in length (Pawlowsky 1924, 1925; Pflugfelder 1930; Vachon 1950; Warburg & Rosenberg 1990; Polis & Sissom 1990, Farley 1996*b*). In *P. mesaensis*, greater surface area for absorption is achieved with much longer trophic tubules that are supported by the ovariuterine tubules and parallel in distribution.

In the evolution of viviparity, embryogenesis is often altered along with maternal reproductive structures (Weekes 1935; Budker 1958; Amoroso 1960; Wourms 1981; Wourms & Lombardi, 1992). This has occurred in scorpions; the sequence and form of organogenesis differs in correlation with the matrotrophic structures of apoikogenic or katoikogenic development (Polis & Sissom 1990; Farley 1996*a*, *b*).

Embryo Spacing

As yet we have no information about the factors that cause certain cells to enlarge and become ova or trophic cells within the germinal epithelium. The ova are initially spaced close together with distances measured in tenths of a millimeter (Figs 2–7). This may reflect an ancestral condition where a large number of eggs were released into the surrounding water (Kjellesvig-Waering 1986; Farley 1996*b*). With viviparity, only a limited number of embryos can develop within the confines of the mesosoma, so many of the ovum protuberances are covered by secondary trophic cells (Figs 6–8) and fail to develop. Eventually, the embryos are separated by more than a millimeter (Fig. 8).

Still unknown for *P. mesaensis* is the number of ova that initially differentiate and form protuberances. An average of 49 embryos were found in gravid females dissected in their third or later year, and about 33 young are released at parturition (Polis & Farley 1979). This is only a fraction of the number of protuberances initially formed, based on spacing observed in the present study. In the buthid *Leiurus quinquestriatus*, the number of protuberances averaged 106 in freshly collected females (Warburg *et al.* 1995).

The spacing of protuberances (Figs 2–5) and embryos (Figs 6–8) raises questions about how reabsorption and continued development are determined along the length of the tubules. Each ovum may secrete one or more chemical substances that initiate differentiation of primary and secondary trophic cells. Enlarging embryos appear to inhibit further development of those nearby (Fig. 7), as though a chemical gradient is involved. The result in *P. mesaensis* is a reduction in embryo number, and regular spacing of the embryos so that each has room to become 11 mm in length and 0.03 g at birth (Polis & Farley 1979).

The limitations of mesosomal space has apparently resulted in an evolutionary trade-off between litter size and embryo growth. The embryos are released early, allowing space for as many young as possible, and further development occurs post-

partum. Within the confines of the mesosoma, the embryos mature to a point where the newborn can climb on the mother's back but not yet capture prey (Polis & Farley 1979; Polis & Sissom 1990). They have a large metabolic reserve, so can increase in length without feeding, and there is further differentiation of sense organs and sting. After 7–20 days (first instar duration in Vaejovidae; Polis & Sissom 1990), the larvae molt and disperse from the mother. For *P. mesaensis* in the deserts of Southern California, the migration of second instars from the maternal burrow can be seen at night (with ultraviolet lights) during the first weeks in August (Polis & Farley 1979).

Acknowledgements

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